Cell Division as a Problem of Pattern in Plant Development*

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The plane in which a cell divides and the position of the new wall laid down between the two daughter cells involve important problems, not alone as to the behavior of individual cells, but also as to the development of multi-cellular plant structures, since the planes of division in a mass of growing tissue must evidently be related to the direction in which growth occurs, and thus to the form of the organs produced.

Various hypotheses have been suggested as to factors which determine the position of the new wall in a dividing cell. Hofmeister showed that such walls are usually formed at right angles to the longer dimensions of the cell. Sachs observed that a new wall tends to meet the old one at right angles. The direction of mechanical pressure, light, electrical currents, and gradients of various chemical substances have been shown to affect the orientation of the division wall. Errera and Berthold, later supported by D'Arcy Thompson and others, maintained that since cell walls in embryonic tissues are thin and semi-liquid, their position is governed by molecular forces and will be such that minimum surface and maximum stability result, so that no more than three walls meet at one point. All these "rules" can be abundantly illustrated from plant material, but every histologist has seen exceptions to them. Some of these have recently been discussed by the writer and Dr. Bloch. The problem is evidently too complex to be explained by any one hypothesis. It has too often been approached simply as a question relating to the activity of single cells rather than of these cells as members of an organized multicellular system. The present paper reports a study of cell division as it occurs in a simple plant structure, in an attempt to determine what relation there may be between the manner in which a cell divides and the position which it occupies in such an organized entity.

The shoot axis of *Equisetum* provides particularly good material for such a study. Its growth is centered in a single apical cell and the lineages of cells arising from this are relatively easy to follow. The structure of the axis is without serious complication and the leaves are small, simple and in whorls. A number of previous studies have been made on various species of this genus and for many of them the development of the shoot apex is well known. It seems worth while, however, to examine the facts for a single

species in some detail from the particular point of view of the problem of cell division.

Equisetum hyemale, one of the larger of our native species, was chosen for study. This has a rather massive meristematic region as compared with some of the more delicate types. Transverse and longitudinal sections, both median and tangential, were cut through the stem tips which had been collected at various times from March until June, the period when meristematic activity and growth are best studied. Cell divisions occur not only at the apex of the meristem near the apical cell, but for some distance back along the axis during the differentiation of various tissues.

The manner in which division takes place was found to differ markedly depending on the location and character of the cells concerned. Some of the types are as follows:

The large apical cell cuts off a daughter cell from each of its three inner faces, successively. The new wall is approximately parallel to the old so that the two daughter cells are dissimilar in shape and usually in size (Fig. 1).

The lower cell elongates, as seen in longitudinal section, and divides periclinally. The inner of its daughter cells contributes, by rather irregular divisions, to a mass of tissue just below the apical cell. The outer one divides anticlinally, and thus parallel to its long dimension. This portion of the meristem thus consists of a surface layer of elongate cells and an inner mass of irregularly-shaped ones (Fig. 1).

Most subsequent divisions in the outer layer are anticlinal, thus violating Hofmeister's rule, with the new division wall straight and parallel with the sides of the mother cell. Occasionally, however, usually at the point where a new leaf primordium will develop, the inner edge of the phragmoplast begins a straight course but before it reaches the end of the mother cell it swerves to one side, usually in the basal direction, until it meets the anticlinal wall of the old cell (Fig. 2). The smaller of the two daughter cells thus produced, somewhat V-shaped in section, will form the apical cell of one of the leaf primordia which begin to appear a little further back. Such a wall as here described is neither across the shorter dimension of the cell nor does it conform to a least-surface configuration, although in the inner part of its course it becomes curved.

Shortly below this level there may be seen in longitudinal section a series of cell divisions across the axis. This marks the beginning of one of the diaphragms which is such a conspicuous feature of the stem anatomy of *Equisetum*. These divisions are always approximately at right angles to the axis regardless of the particular shape of the cells in which they occur and, therefore, occupy positions in these cells which violate many of the "rules."

Such divisions continue until a considerable amount of diaphragm tissue is formed (Fig. 3).

The point where each incipient diaphragm meets the outer surface of the meristem marks the base of a whorl of leaf primordia. While these are still
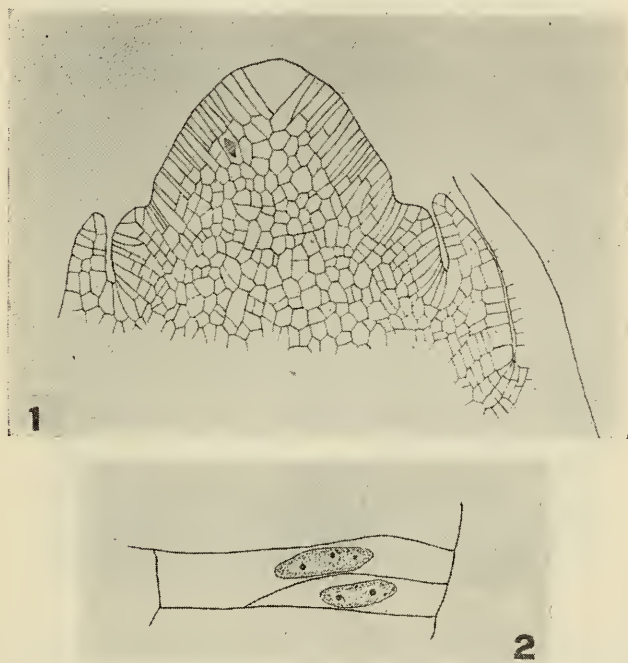

Fig. 1. Section through the extreme tip of the growing shoot of *Equisetum hyemale*, showing apical cell, surface layer of elongate cells, central mass of irregular cells, and young leaf primordia.

Fig. 2. An oblique division in one of the surface cells. The smaller one will produce an apical cell of a leaf primordium.

very small there begins to be differentiated within the base of each a series of provascular strands from which the circle of vascular bundles will later develop (Fig. 3). Each of these strands arises by a series of longitudinal divisions (thus at right angles to those in the diaphragm) in a cell row near the surface of the meristem. These divisions, like those in provascular tissue generally, run parallel to the long axis of the cell.

In the subepidermal layer of the meristem, along the future ridge of the axis, where the photosynthetic tissue will later develop, the method of division is still different. Here the anticlinal longitudinal walls in a given cell are in
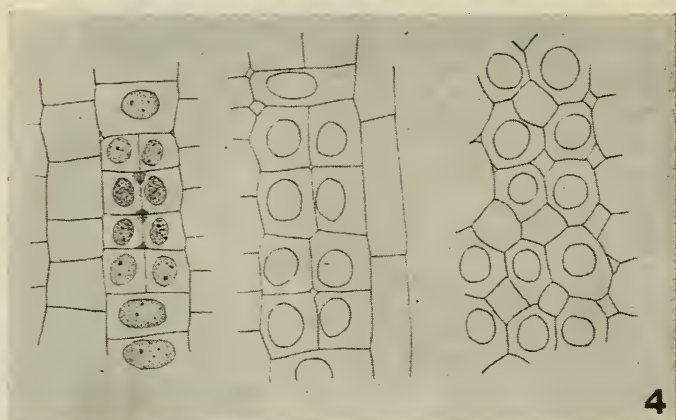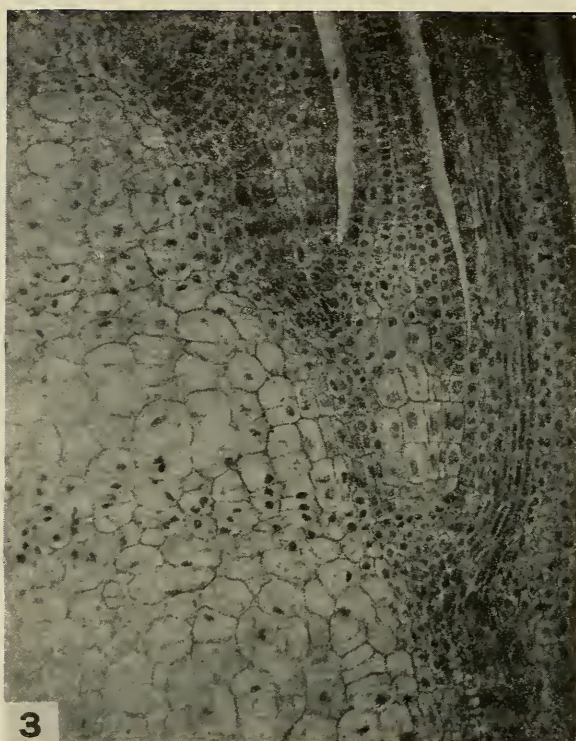
Fig. 3. Photograph through a lower region of the meristem showing parts of several diaphragms, two leaf bases and the beginnings of provascular tissue in stem and leaf.

Fig. 4. Three stages in the development of a row of aerenchymatous tissue. Most of the division walls are opposite those in vertically adjacent cells.

most cases exactly opposite similar walls in the cells above and below, so that in such a group of cells, as seen from its outer surface, four walls usually meet at a point instead of three as in most tissues. The point where these cells come together is evidently subject to a good deal of strain as the cells expand and intercellular spaces thus develop here very early (Fig. 4). These become much enlarged in the mature tissue. The relation between such a type of cell division and the development of aerenchyma has previously been pointed out by the writer.

The surface cells which are to give rise to stomata undergo a remarkable series of divisions. In a vertical row of cells, every second one is a stomatal mother cell. The first division in it is longitudinal and usually unequal, with the new wall convex toward the smaller daughter cell. The next, in the larger cell, is convex in the opposite direction, so that a lens-shaped cell has now been cut out with a larger cell on either side. The lens-shaped cell then divides into two guard cells.

This diversity in the type and direction of cell division in developing plant tissue is of course not confined to *Equisetum* but is a familiar feature of the process of differentiation in all multicellular plants. The important fact which it emphasizes is that no single method of division is universal, and that every "rule" is frequently broken. Evidently many factors may be concerned with determining the plane of cell division. What a given cell will do depends not upon some general principle of division, common to all cells, but upon the conditions which exist at that particular place and time. Every cell is a part of a general developmental pattern, and not only in the way it divides but in every other aspect of its behavior it seems to be governed by its particular place in that pattern. Driesch nearly half a century ago summed this up in his famous aphorism that "the fate of a cell is a function of its position," and Vöchting many years before said the same thing in almost the same words.

This general fact of development, so well illustrated by the controlled diversity of mode of cell division in the meristematic tissues of plants, should be recognized by all students of morphogenesis. In a search for the mechanisms which operate in the remarkable processes of organic development, we tend to oversimplify the problem and to postulate factors which have a specific method of operation. Thus the rôle of auxin, of light, or of a given gene is often assumed to be a definite and invariable one, whereas its effect actually is dependent in very great measure on the internal and external environment in which it operates. In an eagerness to find specific organ-forming substances and stimuli we have too often neglected the complex reaction system, the developmental pattern in which these must work. Knowledge about specific factors is very useful and is rapidly accumulating, but far more important

would be an understanding of the complex organic system in which they work and which determines their effect. About this we still know very little.

The problem may perhaps be stated somewhat more vividly by comparing the operation of a developing organic mechanism with that of others more familiar to us. A nickel inserted into a slot, for example, will activate a turnstile or a juke box or a coin telephone. There is but little specificity in the "stimulus" but a great deal in the mechanism which it activates. If one knew everything about nickels and how they differ from other coins he still would fail to understand how a nickel could produce these results, for an answer to this question lies in the character of the reacting mechanism. In somewhat the same way, auxin produces one effect in one part of the developing organism or under one set of conditions, and quite another elsewhere; and the principle of minimal surfaces may determine the position of new cell walls at one region of the meristem but may be overruled by other factors in another.

The developing organism is a patterned whole, the parts and activities of which derive their particular character from their relation to this whole, and should be studied in this relation and not only as independent structures or processes. An understanding of this organized pattern and the way in which it controls development and differentiation is the chief task of the science of morphogenesis.

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